# *AZTECARPALUS* BALL: NEW SPECIES FROM OAXACA, MEXICO, RE-CLASSIFICATION, AND A RECONSTRUCTED PHYLOGENY OF THE *HEBESCENS* GROUP (COLEOPTERA: CARABIDAE: HARPALINI)

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## Abstract

Described as new from the Mexican state of Oaxaca are *Aztecarpalus hemingi* (type locality 0.8 kil. e. jcts. Rtes. 190 and 125, 2529 m) and *A. whiteheadi* (=*A. liolus* Ball, 1970, not Bates, 1882, type locality Rte. 175, 27.2 kil. s. Valle Nacional, 1097 m). Re-described is *Aztecarpalus liolus* Bates. Keys are provided to distinguish these species from other members of *Aztecarpalus*. A re-classification of the species is presented, based on phylogenetic considerations, and the new species are incorporated as follows: *schaefferi* group- *A. schaefferi* Ball, *A. marmoreus* Ball; *platyderus* group- *A. platyderus* Bates; *hebescens* group- *A. trochotrichis* Ball, *A. hebescens* Bates, and *A. hemingi,* new species; and *liolus* group- *A. lectocolus* Ball, *A. liolus* Bates, and *A. whiteheadi,* new species. A reconstruction of the phylogeny of the *hebescens* group proposes that differentiation of the species was the result of dispersal between, and isolation and differentiation in, various mountain systems in Oaxaca.

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## Introduction

The purpose of this paper is to correct a misidentification based on misunderstanding of the type of *Aztecarpalus liolus* Bates (Ball, 1970: 116), and to propose another species name, as required. I also take this opportunity to describe another species, revise the classification of the genus, and present an hypothesis about the phylogeny of the *Aztecarpalus hebescens* group.

My initial essay on this genus (Ball, 1970) was based mainly on Oaxacan material collected in the eastern part of the Sierra Madre de Oaxaca, the western part of the Mije Highlands, and the Pacific coastal part of the Sierra Madre del Sur, collectively referred to below as the "central area". In 1972 and 1974, I re-visited portions of these areas and collected representatives of some of the species previously described. In 1972, I also visited the eastern part of the Mije Highlands (specifically Cerro Zempoaltepetl (or Zempoaltepec)), the Mixteca Alta, and the adjacent north-central part of the Sierra Madre del Sur (specifically Cerro Yucuyacua). In 1974, I again visited the central areas and the Mixteca Alta (See Fig. 8). In each of the peripheral areas were found species not known from the central area. Although none of these species are represented by more than a few specimens, a pattern seems to emerge, explainable in terms of recurrent cycles of the following elements: dispersal of stocks across lowlands, followed by isolation in separate mountain areas with consequent differentiation, and then re-dispersal. Of course, this is the expected pattern of the events for brachypterous montane species, but by working out the details explicitly it

is possible to bring this small harpaline genus into the mainstream of biology. Unfortunately, not enough information is available to permit a detailed review of evolution for all species groups.

## Material and Methods

Material: The descriptive part of this study is based on 9 specimens collected in 1972 and 1974 and on re-examination of the types of *Aztecarpalus liolus* and of specimens previously assigned to this species (Ball, 1970: 116). The section on phylogeny is based on consideration of this new material, an additional 16 specimens of *A. hebescens* and *A. lectocolus* collected in 1972 and 1974, and on data from the previous study.

Methods: These are the same as described previously (Ball, 1970: 98-100). Ratios and terms are the same, except that the expression "standardized body length" is substituted for "total length". Microsculpture was examined at a magnification of 50X, so the statement "microsculpture effaced" must be understood in this context.

To aid in identification of the new species, a revised key is provided.

## Key to Species of *Aztecarpalus*, Based on External Characteristics

1. Tarsal articles with setae on dorsal surfaces ..... 2.
1′. Tarsal articles with dorsal surfaces glabrous ..... 4.

2(1). Pronotum with postero-lateral angles rounded; elytral microsculpture with lines well developed, meshes transverse.... ..... *A. lectocolus* Ball.
2′. Pronotum with hind angles rectangular; elytral microsculpture various ..... 3.

3(2′). Pronotum with sinuation of sides prominent (Ball, 1970: 105, Fig. 10); elytra with lines of microsculpture effaced..... ..... *A. whiteheadi,* new species.
3′. Pronotum with sinuation of sides short and slight (Fig. 2); elytra of males with lines of microsculpture effaced or faint, of females with lines well developed and meshes transverse.... ..... *A. liolus* Bates.

4(1′). Elytra metallic blue or green, interval 3 of at least one elytron with setigerous puncture on disc ..... 5.
4′. Elytra black ..... 6.

5(4). Elytra metallic green; metepisternum wider than long; hind wings absent ..... *A. trochotrichis* Ball.
5′. Elytra metallic blue; metepisternum longer than wide; hind wings fully developed ..... *A. schaefferi* Ball.

6(4′). Elytron with scutellar stria long ..... *A. marmoreus* Ball.
6′. Elytron with scutellar stria obsolete ..... 7.

7(6′). Dorsal surface of elytron faintly iridescent: microsculpture lines of female very fine, close together, meshes few; of male, lines generally effaced. Male front femur with prominent preapical postero-ventral projection (Fig. 3) ..... *A. hemingi,* new species.

7′. Dorsal surface of elytron not iridescent; microsculpture lines well developed, meshes numerous, generally isodiametric among females, generally transverse among males. Male front femur without projection (Fig. 4) ..... 8.

8(7′). Range—mountains of Puebla and Veracruz .....*A. platyderus* Bates.
8′. Range—mountains of Oaxaca (eastern portion of Sierra Madre de Oaxaca, and western part of the Mije Highlands)..... ..... *A. hebescens* Bates.

## Species Descriptions

### *Aztecarpalus hemingi* Ball, **new species**

Comparisons: Males of *A. hemingi* are unique in form of the front femur (Fig. 3). Among the species characterized by a black dorsum, adult *A. hemingi* are distinctive in having very narrow transverse meshes of elytral microsculpture or lines effaced except basally and apically. In form of the median lobe, male *A. hemingi* and *A. hebescens* are virtually identical but differ in size of spines of the internal sac: in *A. hemingi* males, the spines are uniformly short (Figs. 5B and C); in *A. hebescens,* the spines are of 2 sizes (Ball, 1970: 107, Figs. 28a and b).

Description: Standardized body length, males, 7.84-7.96 mm, females, 7.52-8.08 mm.

**Color.** Dorsum black. Venter and legs, except tarsi, rufo-piceous to piceous; antennae, palpi, and tarsi rufous.

**Setae.** Middle coxae each with 5-11 setae; middle femora each with 5 or more setae ventro-anteriorly. Elytral interval 3 without setigerous puncture. Anal setae (on sternum VII, last normally exposed sternum), 2-3 in males (probably 2 is normal) and 4 in females.

**Microsculpture.** Lines fine, more or less effaced in males. Head, meshes isodiametric; pronotum, meshes transverse; elytra, lines transverse generally not coalesced in form of meshes, in males lines effaced except basally and apically.

**Luster.** Dorsal surface shining, faintly iridescent.

**Head.** Frontal impressions small, punctiform.

**Pronotum.** As in Fig. 1. Sides rather strongly rounded, postero-lateral angles obtuse. Postero-lateral impressions linear.

**Legs.** Anterior tibia with terminal spur broad. Male front tibia gradually narrowed basally, antero-medial surface crenulate, not swollen. Male front tarsus with articles broad (Scape-Tarsal Ratio, 1.50). Scape-Tibial Spur Ratio: male, 1.00; females, 0.89-1.23.

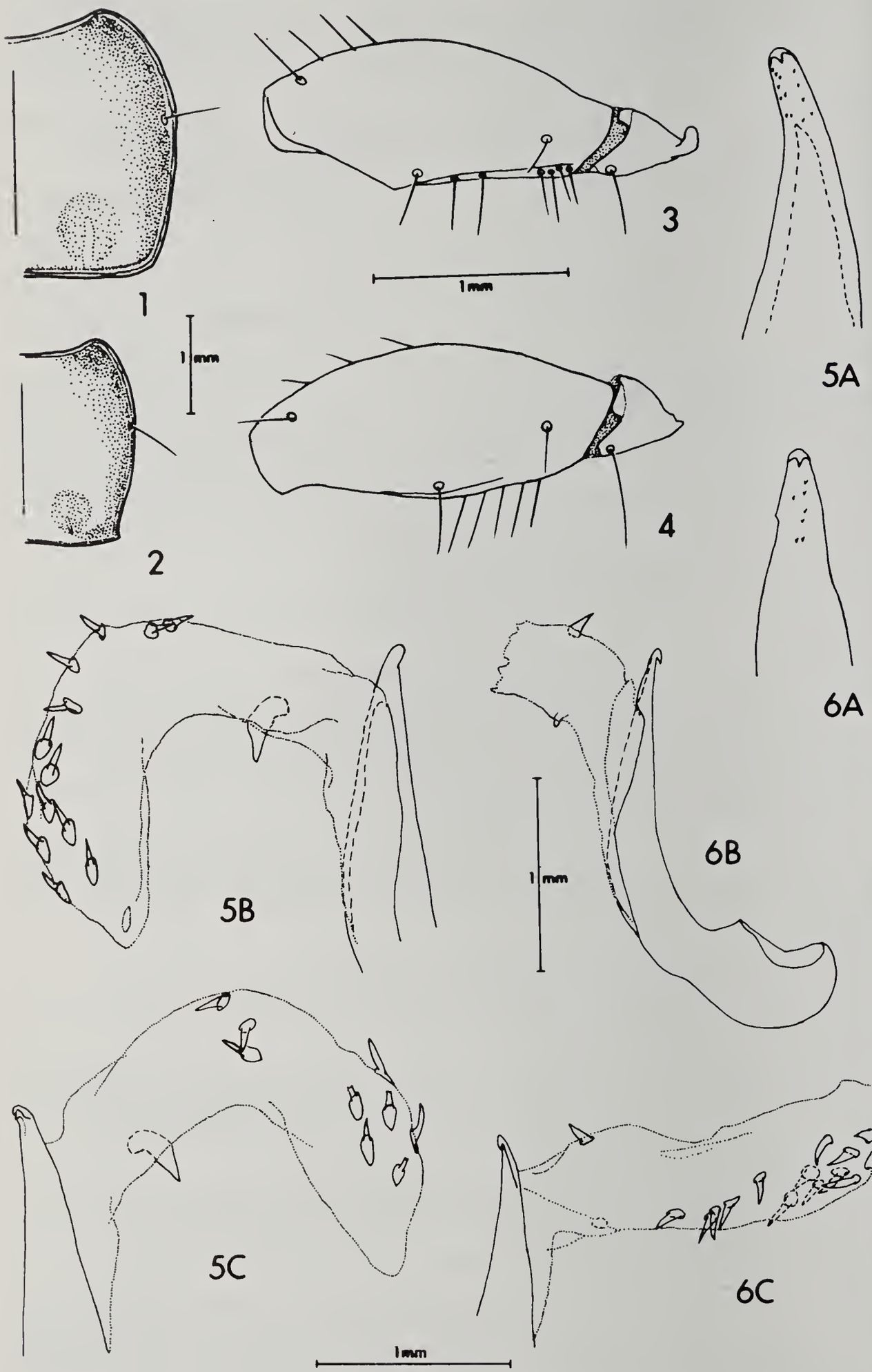
**Metepisternum.** About 1.50 times wider than long.

**Elytra.** Humeri angulate, not denticulate. Striae moderately deeply impressed. Scutellar stria obsolete.

**Hind wings.** Reduced to short stubs.

**Male genitalia.** Median lobe in ventral aspect sinuate, apical portion curved to left; apical portion slender, long, with denticles in 2 irregular rows (Fig. 5A); apex rounded, with short hook ventrally. Internal sac as in Figs. 5B and C; basal spine dorsad, large; medial area with 5 spines; preapical area with 15 spines.

**Female abdomen.** Tergum 10 with apical margin rounded.


1
2
3
4
5A
6A
5B
6B
5C
6C
1 mm
1 mm
1 mm
1 mm

DERIVATION OF SPECIFIC EPITHET: Based on the surname of my thysanopterist colleague, Bruce S. Heming, who, in 1972, shared with me the delights of the long walks on the mountain trails of Oaxaca.

MATERIAL EXAMINED: I have seen 8 specimens of this species. The holotype (male) and allotype (female) are labelled: MEX Oaxaca Microondas Sta. 0.5 mi. e. Jct. Rtes 190 & 125, ca. 2529 m, July 31, 1974; MIDDLE AMER EXP, 1974 D. R. Whitehead, H. Frania & G. E. Ball Collectors. Two female paratypes were collected in the same locality in 1972. One male and 3 female paratypes are labelled: MEX Oaxaca Cerro Yucuyacua, 10300-10900′ (e. Nundaco), August 17, 1972; B. S. Heming, G. E. Ball, collectors. The holotype and allotype are in the United States National Museum. Two paratypes are in the Strickland Museum, University of Alberta. Each of the following institutions has one paratype: British Museum (Natural History); California Academy of Sciences; Museum of Comparative Zoology, Harvard University; and Museum National d'Histoire Naturelle, Paris.

COLLECTING NOTES: The specimens were found on the ground, under cover, in or at the edges of rather dry oak forests at high elevations. The 2 localities (Cerro Yucuyacua and the "microondas" (=microwave tower station)), are within 60 kilometers of one another, measured in a straight line. One specimen collected on Cerro Yucuyacua is partially teneral.

GEOGRAPHICAL AFFINITIES: This species is allopatric to all other known species of *Aztecarpalus* (Fig. 8). It occurs in an isolated section of the Sierra Madre del Sur adjacent to the Mixteca Alta. Southeastward, this area is cut off from high areas by the lowlands of the Rio Verde Basin, specifically the valley of the Rio Cuañana. Northeastward, the area is isolated from the Sierra Madre de Oaxaca and the Mije Highlands by the valley of the Rio Grande.

RELATIONSHIPS: Probably *Aztecarpalus hebescens* is the closest relative of *A. hemingi*. See "Evolutionary considerations", below.

### *Aztecarpalus liolus* Bates

*Harpalus liolus* Bates 1882: 58. Type material in Oberthür Collection, Box No. 225 (Museum national d'Histoire naturelle, Paris). HOLOTYPE male, labelled: Mexique; A. Deyrolle; Ex Musaeo Chaudoir [red print].
*Trichotichnus liolus* Csiki 1932: 1220.

NOTES ON OBERTHÜR MATERIAL: Ball (1970: 116) mis-identified 3 specimens of another species (*A. whiteheadi,* new species) as members of *A. liolus*. Details are provided below.

Next to the holotype in Box 225 is a female labelled: Mexico Flohr; Harpalus liolus Bates, (female sign).

COMPARISONS: Adults of *A. liolus* and *A. whiteheadi* are very similar to one another, differing in external characteristics as indicated in the above key. If it were not for differences in form of male genitalia (Fig. 6A and B; cf. Ball,

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Fig. 1-2, Pronotum, right half, dorsal aspect: Fig. 1, *A. hemingi*; Fig. 2, *A. liolus*. Fig. 3-4, Left front trochanter and femur of male, posterior aspect: Fig. 3, *A. hemingi*; Fig. 4, *A. hebescens*. Fig. 5-6, Male genitalia (A, median lobe, apical portion, ventral aspect; B, median lobe, apical portion, and everted internal sac showing spines but not microtrichia, left lateral aspect; C, same, right lateral aspect): Fig. 5, *A. hemingi*; Fig. 6, *A. liolus*.

1970: 106, Figs. 23a and b), I might not consider the 2 forms as specifically different, although the habitat difference would play an important role in inferring systematic relationships (see "Collecting notes" for details).

DESCRIPTION: Standardized body length, males 6.04-7.16 mm., female 6.56 mm.

**Color.** Body rufo-piceous. Following rufo-testaceous: antennae, maxillae, and labium. Legs generally piceous, tarsi rufo-piceous to piceous.

**Setae.** Dorsal surfaces of tarsomeres each with few long setae. Middle femur with 5 setae antero-ventrally. Middle coxa with 4-5 setae. Interval 3 of each elytron without setigerous puncture. Anal setae, 2 in male and 4 in female.

**Microsculpture.** Lines on dorsum very fine, more distinct in female than in males. Meshes on head isodiametric, on pronotum and elytra transverse, very narrow, almost effaced on males.

**Luster.** Surface shining, elytra of female very faintly iridescent.

**Head.** Frontal impressions shallow, punctiform, without shallow groove directed toward compound eye.

**Pronotum.** As in Fig. 2, sides posteriorly briefly sinuate or evenly incurved. Postero-lateral angles rectangular.

**Legs.** Anterior tibia with terminal spur broadened. Male front tibia with antero-medial surface near base not crenulate, not swollen. Scape-Tarsal Ratio 1.60-1.80. Scape-Tibial spur ratio, males 1.28; female, 1.12.

**Metepisternum.** About 1.25 times wider than long.

**Elytra.** Striae moderately impressed; scutellar stria obsolete. Intervals 7 and 8 subcarinate before apex, other intervals flat throughout.

**Hind wings.** Absent.

**Male genitalia.** Median lobe in ventral aspect as in Fig. 6A, sinuate on left side; apical portion straight, broader than in *A. whiteheadi* (cf. Ball, 1970: 106, Fig. 23a), moderately long, with few and very small denticles and short apical hook. Internal sac (Figs. 6B and C): basal spine small, not strongly curved; medial area with 6 spines, preapical area with 9 spines.

**Female abdomen.** Tergum 10 with apical margin rounded.

COLLECTING NOTES: A single male of this species was found on the southwestern slope of Cerro Zempoaltepetl (Fig. 8) at an elevation of 2652 m, in a fallow field that had been cultivated within a year or so. The area had probably supported at one time an oak-pine forest. The carabid fauna was varied, including an assortment of both woodland and meadow-inhabiting taxa. See Ball (1973: 156) for additional details on this area.

DISTRIBUTION: This species is known certainly only from Cerro Zempoaltepetl, Oaxaca.

MATERIAL EXAMINED: I have seen only 3 specimens: 2 in the Oberthür Collection (see above) and a male labelled MEX Oaxaca Cerro Zempoaltepetl 8700-10500′, August 20, 1972; B. S. Heming, G. E. Ball Collectors (University of Alberta, Strickland Museum).

GEOGRAPHICAL AFFINITIES AND RELATIONSHIPS: See these topics under *A. whiteheadi,* below.

*Aztecarpalus whiteheadi,* new species

*Aztecarpalus liolus* Ball, 1970: 116 (not Bates, 1882: 58).

Adults of this species most closely resemble those of *A. liolus* but are

adequately distinguished in the above key. The most distinctive structural feature is the form of the median lobe: that of *A. whiteheadi* lacks ventral denticulations and the left lateral margin is not markedly sinuate (Ball, 1970: 106, Figs. 23a and b).

I have nothing to add to the previous description of this species, under the name *A. liolus* Bates.

Derivation of specific epithet: From the surname of Donald R. Whitehead, who collected one of the type specimens, and recognized it at once as a remarkable harpaline.

Material examined: HOLOTYPE male, labelled: MEXICO Oaxaca 16.9 mi. s. Valle Nacional 3600′, V.4-5.1966; G. E. Ball, D. R. Whitehead, collectors. A female allotype and male paratype are similarly labelled.

The holotype is in the United States National Museum; the allotype is in the Museum of Comparative Zoology, Harvard University; and the male paratype is in the Strickland Museum, University of Alberta.

Geographical affinities: The specimens of this species were collected at a lower elevation than members of any other Oaxacan species, in the Sierra Madre de Oaxaca. Parapatric with this species are *A. hebescens* and *A. trochotrichis,* both of which inhabit the same mountain range but at higher elevations (see Fig. 8). Allopatric with *A. whiteheadi* are *A. liolus* and *A. lectocolus,* also included in the *A. liolus* species group.

Relationships: This species and *A. liolus* are probably sister species, sharing in common an apotypic pronotal form and reduced elytral microsculpture. Of the 2, *A. whiteheadi* seems more apotypic in structural features. The third member of the *liolus* species group, *A. lectocolus,* is the most plesiotypic, with rounded hind postero-lateral angles of the pronotum and well developed dorsal microsculpture. All 3 species are allopatric, and the range of *A. lectocolus* is the most extensive.

## Evolutionary Considerations

Included in this section are a revised classification of the species of *Aztecarpalus* based on a phylogenetic analysis and a detailed phylogenetic treatment of the *A. hebescens* species group.

Classification of *Aztecarpalus*: The arrangement originally proposed was probably incorrect, the *hebescens* group being based on symplesiotypic character states (elytral microsculpture isodiametric, color of dorsum black) and the shared apotypic similarities of *A. hebescens* and *A. trochotrichis* disregarded, with the latter species placed in a group by itself. I believe now that *A. trochotrichis* and *A. hebescens* belong in the same group. From this group, *A. platyderus* is excluded and placed in a group of its own. I also think that the *schaefferi* group is the sister group of the other taxa of *Aztecarpalus.*

I prefer not to present a detailed phylogenetic treatment at this time, but the general trend of the argument is summarized in the following key to groups. The sequence of groups is believed to be phylogenetic. Each couplet gives plesiotypic and apotypic character states for 1 or 2 characters, the apotypic state indicated by an asterisk. Names of included species are listed in parentheses, following the name of the group.

1. Scutellar stria long; internal sac of male genitalia with basal sclerite*; distribution, Sierra Madre Oriental and northeastern Trans-Volcanic Sierra *schaefferi* group (*A. marmoreus; A. schaefferi*).

1′. Scutellar stria short*; internal sac of male genitalia without basal sclerite; distribution, southeastern Trans-Volcanic Sierra and mountains of Oaxaca ..... 2.

2(1′). Internal sac of male genitalia with apical spine*; distribution, southeastern Trans-Volcanic Sierra..... ..... *platyderus* group (*A. platyderus*).

2′. Internal sac of male genitalia without apical spine; distribution, mountains of Oaxaca* ..... 3.

3(2′). Male genitalia, median lobe inclined to left apically*; tarsi with dorsal surfaces glabrous..... ..... *hebescens* group (*A. trochotrichis; A. hebescens; A. hemingi*).

3′. Male genitalia, median lobe straight in ventral aspect; tarsi with dorsal surfaces sparsely setose*..... .....*liolus* group (*A. lectocolus; A. liolus; A. whiteheadi*).

TABLE 1. PHYLOGENETIC INTERPRETATION OF CHARACTER STATES OF THE *Aztecarpalus hebescens* SPECIES GROUP.

| NUMBER | CHARACTER | INTERPRETATION OF CHARACTER STATE PLESIOTYPIC | APOTYPIC |
|---|---|---|---|
| 1 | color: dorsum | black | metallic |
| 2 | male hind trochanter | bisetose | plurisetose |
| 3 | male anal setae | 2 | 4 |
| 4 | microsculpture: male elytra | meshes clearly indicated | meshes effaced over most of surface |
| 5 | male median lobe: apical portion | broad | a. narrower<br>b. narrowest |
| 6 | elytron: discal seta | present | absent |
| 7 | male front femur | without projection | with projection |

Because character distribution is so complex among the known species of *Aztecarpalus* and so much convergence must be accounted for, I am not yet prepared to present an analysis of this topic for the whole genus. However, the phylogenetic pattern for the *hebescens* group seems interpretable, and details are presented below.

PHYLOGENY OF THE *A. hebescens* GROUP: Characters on which this analysis is based are numbered and listed in Table 1, with plesiotypic (ancestral or closest to it) and apotypic (derived) conditions indicated. The sequence provides a maximally dense grouping of apotypic character states for each species (see Fig. 7). Character 4 is 3-state, and the others are 2-state. States of characters 1 to 4, 6, and 7 were classified generally by comparison with a generalized hypothetical member of the subtribe Harpalina: thus, for most

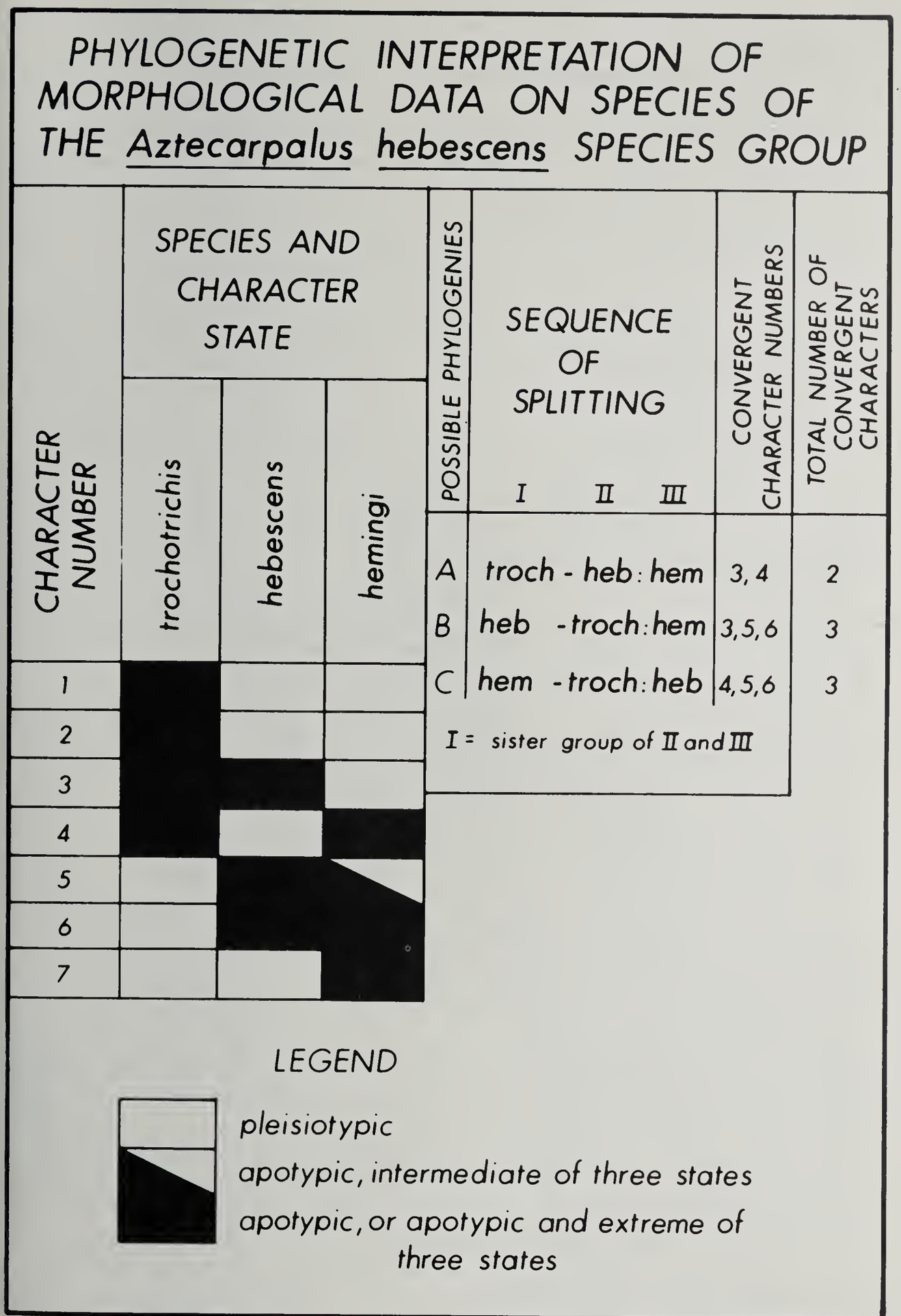


Fig. 7. Phylogenetic interpretation of morphological data on species of the *Aztecarpalus hebescens* species group.

characters, states listed as plesiotypic are of more frequent occurrence in the Harpalina than are states listed as apotypic. For the median lobe (character 5), the "broad" form is considered as plesiotypic because this seems to be the commonest character state in *Trichotichnus,* the sister group of *Aztecarpalus.* Presumably, therefore, the "broad" form is shared among members of these 2 genera because it was inherited from their common ancestor. Nonetheless, the median lobe of *A. trochotrichis,* though classified as broad and hence as plesiotypic, is probably not identical in details of form to the median lobe of the ancestral stock of the *A. hebescens* group; rather, it is closer to the ancestral condition than to the detailed forms of median lobes of *A. hebescens* and *A. hemingi.* In turn, the detailed form of the median lobe of the *A. hebescens* group ancestral stock was probably like that of *A. platyderus* (Ball 1970: Fig. 21), the condition that I imagine to be most plesiotypic in the genus.

With 3 species, 3 phylogenies are possible (Fig. 7), the most parsimonious being the one of choice—unless there is evidence to the contrary. Phylogeny "A" requires only 2 instances of convergence, whereas "B" and "C" require 3, each. Thus, Phylogeny "A" is accepted, with *A. trochotrichis* as the sister group of the stock that gave rise to the other 2 species. According to this scheme, microsculpture of the elytra has been reduced twice, and male anal setae have increased from 2 to 4, twice.

The distribution pattern provides another clue to understanding phylogeny of the *hebescens* species group. In its simplest terms, *A. trochotrichis* and *A. hebescens* are probably sympatric (they have not been collected in the same locality, but their ranges overlap extensively), both occurring in adjacent portions of the Sierra Madre de Oaxaca (Capulalpam) and in the Mije Highlands. In the more distant Mixteca Alta and central portion of the Sierra Madre del Sur is *A. hemingi.* These 3 species occur at elevations in excess of 2460 m. (Capulalpam is lower, but probably specimens were collected in the surrounding hills, rather than right in town.) The species *A. trochotrichis* may be in wetter areas than the other 2 species, but generally the 3 are in similar places: meadows and rather open oak or pine-oak forests.

Development of the pattern cannot be explained solely in terms of the extant species, nor in terms of their present known ranges. Rather, present discontinuity of range is evidence for past continuity; and, for sister pairs, present continuity is evidence for past discontinuity. To allow potential continuity between isolated ranges of members of this group, climatic conditions would have to be such that the species could live at lower elevations, and hence could enter areas geographically intermediate between the present ranges. Such conditions might also have allowed dispersal of the ancestral stock from further north. (Reasons for believing that *Aztecarpalus* originated further north are given by Ball, 1970: 122). Because most species of the genus are on the eastern slopes of the Mexican mountain systems, it seems reasonable to suggest that initial dispersal took place in this area.

Thus, the following scenario is presented in numbered steps as a recurring cycle of: dispersal; isolation, with consequent differentiation leading to allopatric taxa; and re-dispersal, leading to sympatric or parapatric taxa. The sequence is best followed with reference to Fig. 8. Names for the areas on this map are from West (1964: 63-64). The base map is from "Caminos de Mexico", Map 28 (Anon., 1964).

1. Entry of the ancestral stock of the *hebescens* group into the Sierra Madre de Oaxaca and Mije Highlands, from the Trans-Volcanic Sierra.
2. Isolation therein, and differentiation.

3. Dispersal westward across intervening lower lands into the Mixteca Alta—central Sierra Madre del Sur region. (If the group dispersed southward across or around the central part of the Valley of Oaxaca, no evidence of such movement has been found.)

4. Isolation of stocks in the more eastern Sierra Madre de Oaxaca-Mije Highlands, and in the more western Mixteca Alta-Sierra Madre del Sur ranges.

5. Differentiation, with the eastern refugium isolate giving rise to *A. trochotrichis,* and the western one to the *A. hebescens-A. hemingi* ancestor.

6. Re-dispersal of the latter stock.

7. Isolation of this stock in the western and eastern refugia.

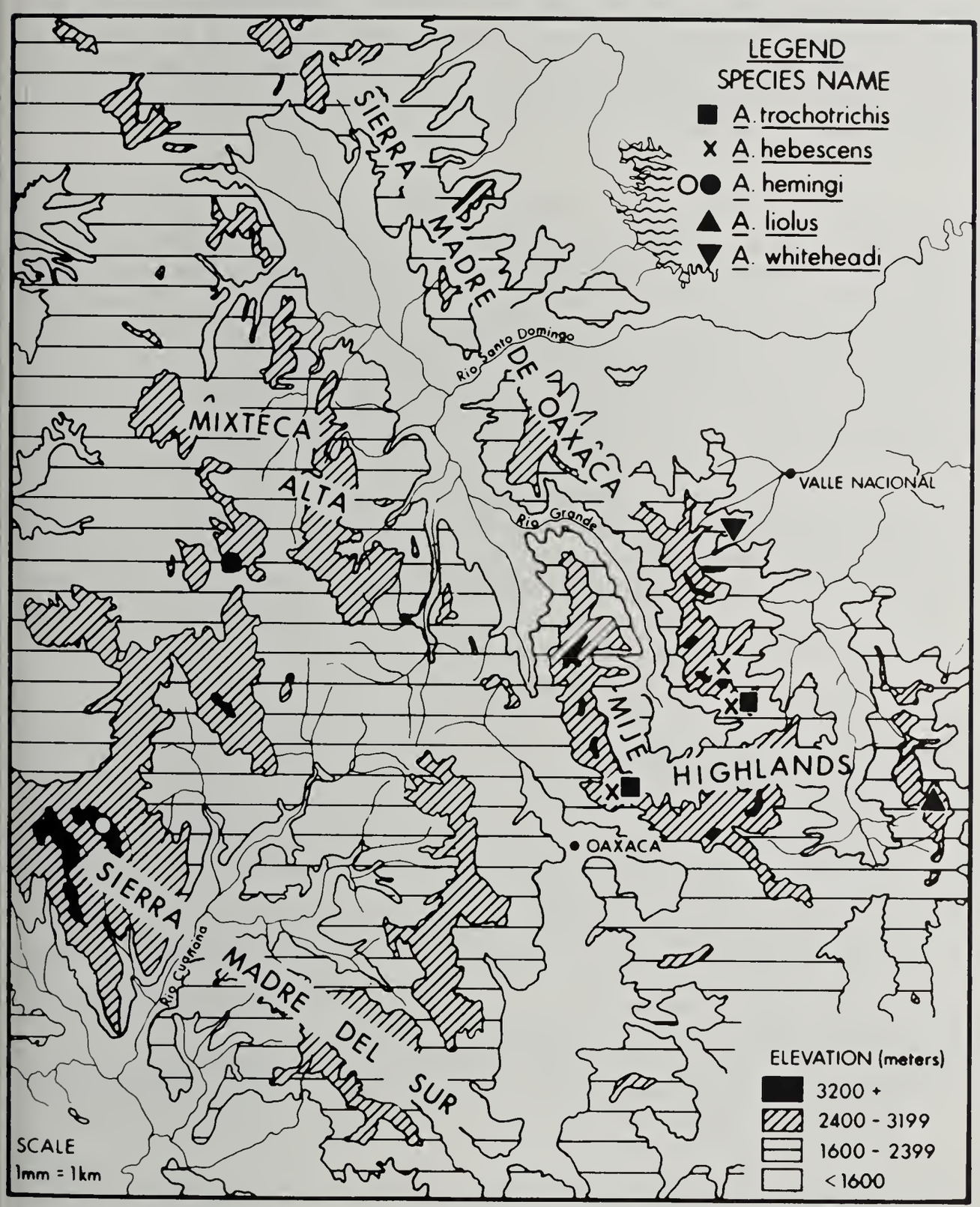


Fig. 8. Map of a portion of the Oaxacan Highlands, showing the known distribution of five species of *Aztecarpalus.*

8. Differentiation, to produce *A. hemingi* in the western refugium and *A. hebescens* in the eastern refugium.

This hypothesis explains the pattern of relationships and distribution as it is presently known. It does not explain why *A. trochotrichis* failed to reach the Mixteca Alta when the *A. hebescens-A. hemingi* stock was able to disperse to the Mije Highlands, nor does it explain why the range of the *hebescens* group is as restricted as it seems to be. The hypothesis does not emphasize the potentially important role that extinction may have played, mainly because of the limited evidence available about this topic.

The hypothesis provides a model for study of other groups of montane species in Oaxaca, comparable to the models for speciation in the Trans-Volcanic Sierra based on *Calathus* (Ball and Nègre 1972), and in the mountains of Guatemala and Chiapas, based on *Cyrtolaus* (Whitehead and Ball 1975). It remains to test these models thoroughly, in terms of additional material of the model groups, in terms of other insect groups, and in terms of implicitly predicted climatic changes and shifts of vegetational zones.

## Acknowledgments

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